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BIOLOGICAL STUDIES ON CORYMORPHA. IV.¹

BUDDING AND FISSION IN HETEROMORPHIC PIECES AND THE CONTROL OF POLARITY.

HARRY BEAL TORREY.

The large solitary hydroid *Corymorpha* exhibits the phenomenon of heteromorphosis in forms even more striking than those under which it appears in the related *Tubularia*. At the same time, its normal polarity is in several respects more obviously marked. As against a stem, in *Tubularia*, that presents little or no indication of axial differentiation, the column of *Corymorpha* is divided into several regions sharply characterized by differences in form, structure and function. Its diameter varies, being greatest near the base, which is enveloped, for about one third the total length, in a thin layer of perisarc. Beyond the edge of the latter, the naked ectoderm is thicker, its cells are more narrowly columnar, and there is a marked increase in the number of nematocysts. Within the perisarc is the zone of frustules, or rootlets, that form the holdfast and have been homologized with the stolonal processes of *Tubularia*, although they are far more specialized structures. The proximal extremity, conical in form, is furnished with an amoeboid ectoderm, by means of which the polyp creeps about.

Not only in structure does one find evidence of regional differentiation, but in capacity for regeneration as well. A hydranth is replaced after section of the column, with a velocity that decreases with the distance from the distal end of the intact hydroid. The differences in velocity are so slight as to be appreciated with difficulty in the distal half of the column, but are easily recognizable in a comparison of rates of regeneration in distal and proximal thirds. Furthermore, heteromorphosis,

¹Contribution 32 from the Laboratory of the Marine Biological Association of San Diego. Preceding numbers of the Biological Studies on *Corymorpha* have appeared as follows: I., *C. palma* and Environment, *J. E. Z.*, 1 (1904), p. 395; II., The Development of *C. palma* from the Egg, *Univ. Calif. Publ. Zool.*, 3 (1907), p. 253; III., Regeneration of Hydranth and Holdfast, *ibid.*, 6 (1910), p. 205.

though it may occur after section of the column even below the frustular zone, in the extreme basal region, is most frequent in pieces cut from the column in its distal half.

At the very beginning of my observations on the regeneration of *Corymorpha*, I was struck with two facts: (1) that a segment from the distal half of the column and including the hydranth, does not develop a hydranth at the proximal end until the original hydranth is removed; (2) that when the original hydranth has been removed, the proximal hydranth develops, under normal conditions, more slowly than the distal—another indication, it may be mentioned, in passing, of the initial polarization of the column.

These facts suggested the possibility that, by delaying the development of the distal hydranth on a regenerating piece until the proximal hydranth should have reached an advanced stage of development, the initial polarization might be completely reversed. Accordingly, in the summer of 1902, I performed the following experiment.¹ A segment was cut from the distal half of an average polyp (Fig. 1, A). It was then inverted, and the distal cut surface held against the glass bottom of the aquarium by the weight of a steel needle through the distal region (Fig. 1, B). The proximal end was free and the stem vertical. At

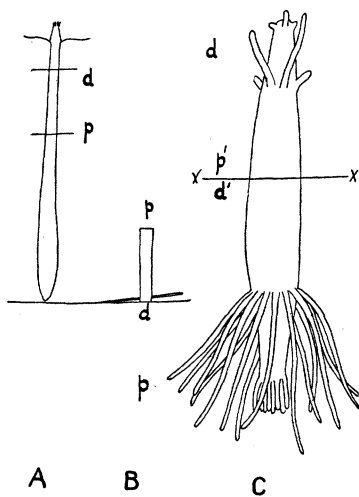


FIG. 1.

the end of three days, a hydranth flourished at *p*, though there was sign neither of tentacles nor frustules at *d*. The needle was removed. Two days later a small hydranth had appeared at *d* (Fig. 1, C), with three distal and four proximal tentacles, somewhat irregularly arranged, probably owing to the wound left by the needle and to other adverse conditions to which that end may have been subjected when pressed against the substratum.

¹All the regenerations noted in this paper occurred under starvation conditions.

It will be noted that while a distal hydranth failed to develop in contact with the substratum, it soon appeared when freed from this contact, in spite of the presence of the large proximal hydranth. On the supposition, however, that the result may not have fully indicated the real state of affairs in the heteromorphic segment, the latter was sectioned at the level x . In two days frustules were appearing at p' ; the original polarity of this portion of the column was preserved. But frustules were also appearing at d' , and two days later, were unmistakably defined. *In this latter region, therefore, the original polarity was reversed; on a segment of a given polyp, not only had hydranth appeared in the customary position of holdfast, but holdfast had appeared in the customary position of hydranth.*

The outcome of this experiment recalls the reversal of polarity which Loeb later obtained in *Tubularia crocea* when, after accelerating the development of the proximal hydranth by inhibiting the development of the distal, he cut a segment just distal to the proximal hydranth and found that a proximal was now produced more rapidly than a distal hydranth.¹ Morgan and Stevens obtained a similar result on *T. marina* although the polarity of the stem was reversed for but a very short distance from the proximal end in this species.²

II.

The suggestion, coming from the above experiment with *Corymorpha*, that section of the column between the hydranths merely disclosed a reversed polarity that already existed but was not, under the conditions, expressed in structural differentiation, led to a number of similar experiments which showed that the original result was in no sense exceptional. I will consider three series of these experiments.

In the first, nine heteromorphic pieces were sectioned at different levels to determine the extent to which each hydranth might control the intermediate region in regeneration. In no. 1, the distal hydranth was removed by a cut immediately below it

¹Pflüger's *Arch.*, 102 (1904), p. 152; trans. in *Univ. Calif. Publ. Physiol.*, 1 (1904), p. 151.

²*J. E. Z.*, 1 (1904), p. 559.

(Fig. 2, *a*); it was replaced by another hydranth that at the end of ten days was in the condition shown in Fig. 2, *b*. No. 2 was a similar case. In neither of these cases was reversal exhibited. No. 3 died. No. 4 is represented in Fig. 3, the proximal hydranth being much less developed than the distal, and the plane of section passing near but not immediately distal to it. In four days both

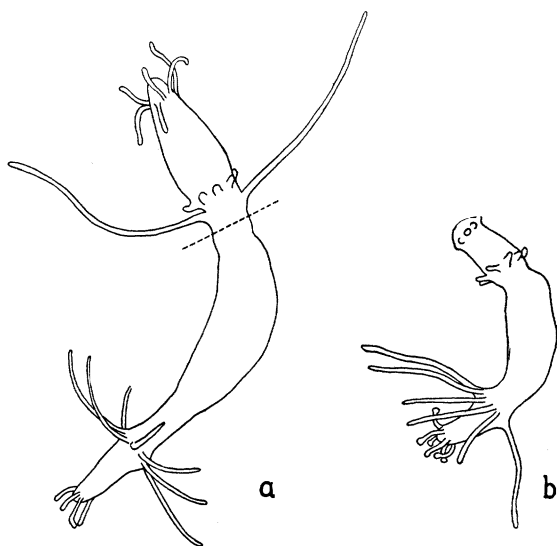


FIG. 2.

segments possessed frustules; the proximal segment had, accordingly, reversed completely. No. 5 (Fig. 4) exhibited another case of complete reversal in the proximal segment; both segments were as shown in Fig. 5 at the end of five days. No. 6 was a similar case. No. 7, cut when in the condition shown in Fig. 6, appeared, five days later, as shown in Fig. 7. No. 8, a similar case, exhibited similarly a complete reversal in five days. No. 9 resembled Fig. 2, *a*; but it was the smaller, *proximal* hydranth that was removed, by a cut immediately distal to it; in seven days a new hydranth was established in its place.

According to these results, heteromorphic pieces produce hold-fasts at the wound when sectioned approximately midway between the hydranths, but produce hydranths at the wound on the longer pieces in those cases in which either hydranth has been removed by a cut immediately below it.

The second series of experiments involved 14 heteromorphic pieces whose proportions and stage of development are represented in the accompanying diagrams (Fig. 8). These pieces were cut as indicated in the diagrams. Four days later, both parts of *a*, *c*,

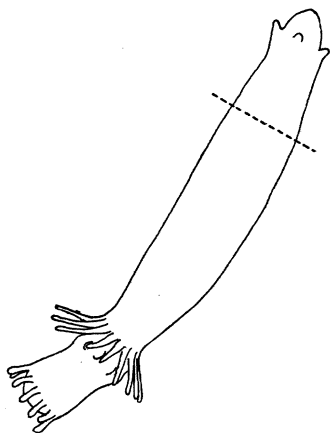


FIG. 3.

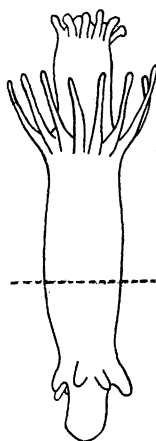


FIG. 4.

d, *e*, *f*, *h*, *i*, *l*, were attached and possessed frustules; the polarity of one of the pieces in each of these cases, accordingly, was completely reversed. At the same time, both portions of *b* were

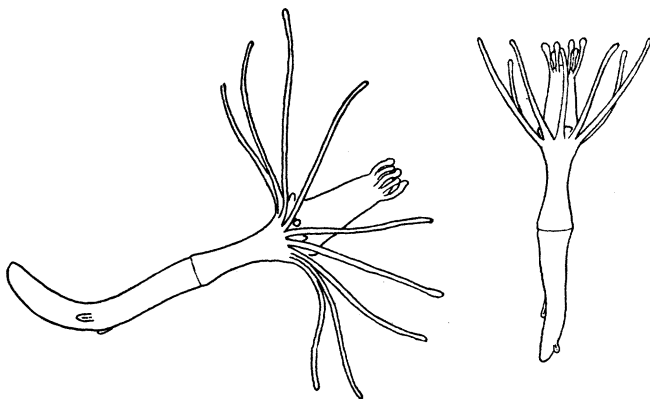


FIG. 5.

regenerating as single polyps, one being attached and furnished with frustules, the other being unattached and lacking frustules. Under *g*, four heteromorphic pieces were grouped. Four days

after cutting, all were regenerating as single polyps, six being attached and possessing frustules, two being unattached and lacking frustules. Both pieces of *k* were attached, three days after

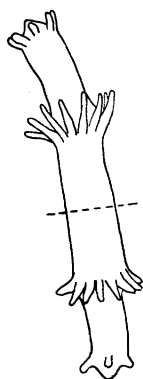


FIG. 6.

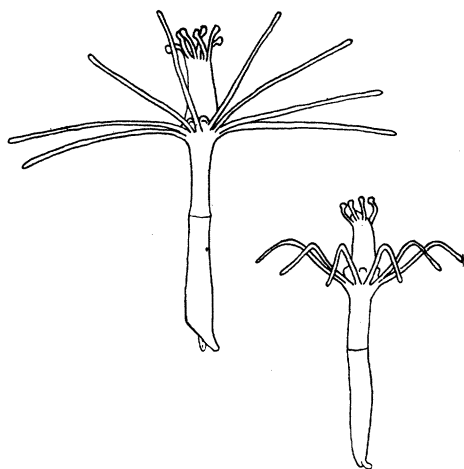


FIG. 7.

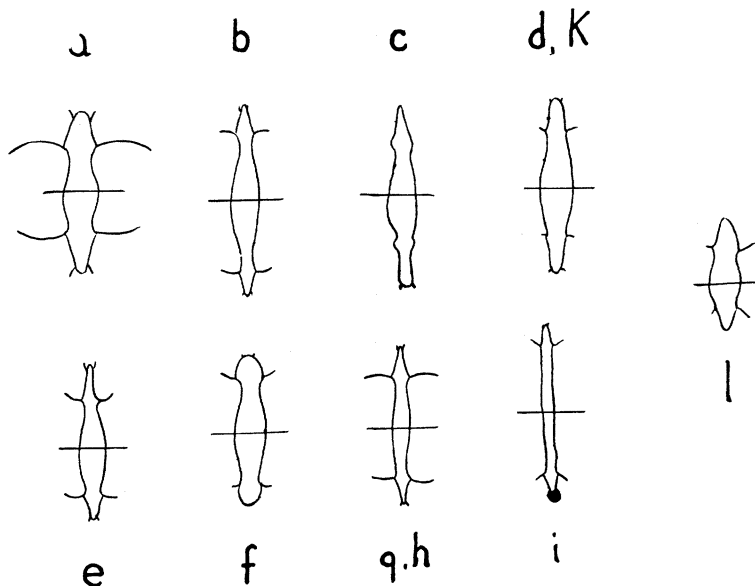


FIG. 8.

cutting, but owing to accidental neglect, disintegrated before forming frustules.

It should be noticed especially that all the heteromorphic pieces used in this series were *short*, and none were above medium diameter. *In not a single case, under these conditions, did the polarity fail to reverse in one of the portions into which the heteromorphic pieces were divided.*

The third series shows the importance of this consideration of length. Three heteromorphic pieces, absolutely and relatively much longer than those of the second series, one of them considerably larger than the other two, were sectioned as shown in Fig. 9. Five days after section, all six pieces were heteromorphic which indicated that in none of them, whether distal or proximal, was development at the wound dominated by the conditions, existing at the other end of the piece.

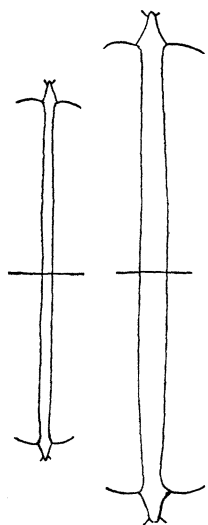


FIG. 9.

The same fact is brought into clear relief by a comparison of the following figures. Of 14 segments representing the distal half of the column of 14 polyps of moderate size, 12 were heteromorphic in 3 days. Of 81 very short segments from several small polyps, only 6, or 7.4 per cent., became heteromorphic. Further, of 13 segments of approximately the same length and diameter as the pieces obtained by cutting the heteromorphic pieces in series 2, 8 became heteromorphic. Of 15 similar segments, 10 became heteromorphic.

Besides these figures, there is a mass of evidence, obtained by repeated experiments on large numbers of individuals, demonstrating that the presence of the original hydranth on a segment of the column inhibits the development of a proximal hydranth.

It is clear, then, in the light of the facts cited in this section, (1) that *reversals of polarity profound enough to effect entire segments of the column as units are readily produced in Corymorpha*; and (2) that *the stage of differentiation at one end of a piece will under certain conditions control differentiation at the other end.* That reversals of polarity, in cases of heteromorphosis, are often shown, by form changes, to affect considerable areas of the column, without aid from the knife, will appear in the following section.

III.

As the first evidence in this direction I may refer at once to certain U-shaped figures formed from heteromorphic segments by the attachment of the latter to the bottom of the aquarium dish by means of adhesive ectoderm developed on one side of the column. Such a case is shown in Fig. 10, which represents the condition of a segment sixteen days after its removal from the distal half of a column. A constriction defines the aboral limits of the regenerating polyps. Frustules are present in two groups,

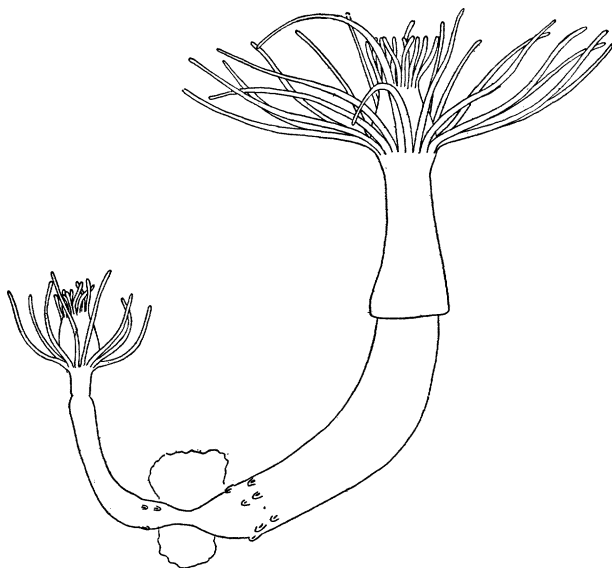


FIG. 10.

roughly proportional in numbers to the sizes of the polyps to which they belong, and situated in the position normally occupied by frustules in the adult. The smaller polyp approaches more closely to the proportions of the larva. On the following day, this process of fission had been completed, probably by rupture, although the proximal ends of the two polyps were then rounded and smooth without traces of such a process.

Through my failure, after repeated attempts, to obtain many cases of fission of this sort, I found that a necessary element in the process was the adherence of the heteromorphic piece to the

substratum. I pointed out some years ago¹ that *Corymorpha* is negatively geotropic, even small fractions of the column reacting with great definiteness. This tendency to bend away from the center of the earth can be effective, however, only when the reacting piece is properly anchored. Pieces free from the

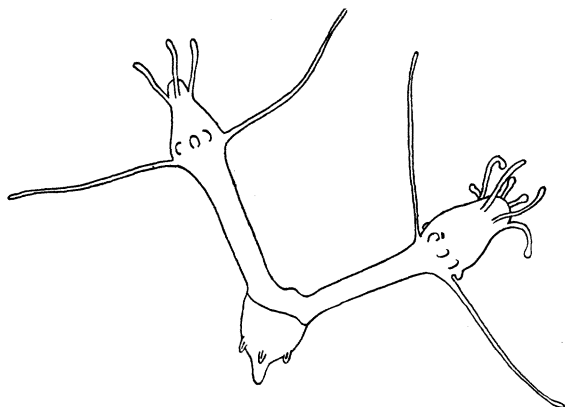


FIG. 11.

substratum never exhibit the reaction. As soon as they are attached, it appears; and U- and Y-shaped figures are formed when pieces are heteromorphic and the point of attachment is between the developing ends.

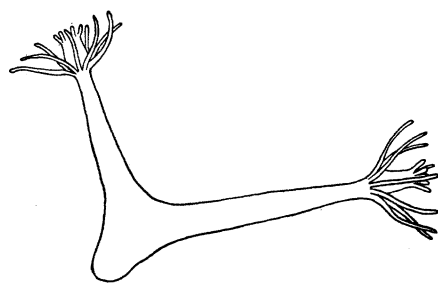


FIG. 12.

Each Y-shaped figure is formed from a straight piece by the development of a protuberance that corresponds to the stem of the Y, and is terminally adhesive (Figs. 11, 12, in both of which the limbs of the Y have become much attenuated during the

¹J. E. Z., 1 (1904), p. 395; *Univ. Calif. Publ. Zool.*, 2 (1905), p. 335.

development). Such protuberances and Y-shaped figures are found in nature only in the most exceptional cases, where they probably arise in response to the same conditions that bring them forth in the laboratory. To present these conditions with sufficient fullness, I must refer briefly to other abnormal forms that have often appeared in neglected aquaria.

It was often difficult, in warm weather, in the absence of running water, to prevent the growth of bacteria in the dishes in which freshly collected polyps were placed. Under the influence of fermentative changes induced by these conditions, the hydranths would cast their large proximal tentacles and medusiferous peduncles, the distal tentacles would be absorbed, and the column would come rapidly to be surmounted by a more or less rounded mass of tissue that might show two or three knobby irregularities. The columns were affected in a much less degree if at all. In fact it is quite easy to avoid these difficulties altogether by removing the hydranths as soon as the polyps are collected. This fact is doubtless due to the relatively large mass of protoplasm in, and the greater differentiation of the tissues of the hydranths.

Upon the reduction of the hydranths to the knobby masses just mentioned, and the removal of the débris composed of disintegrating tentacles and medusæ with their peduncles, the bacteria would disappear, fermentative processes would lead to the substitution, for the original hydranths, of various monstrous forms—double hydranths, hydranths with double or triple probosces in varying degrees of independence, combinations of hydranths with varying numbers of probosces, etc. These phenomena indicated the breaking up of the original single physiological system into several, the first sign of this multiplication appearing in the irregular form of the terminal mass of tissue. Each irregularity was the center of a budding process. And without laying any emphasis on the manner of its initiation, each budding process may be compared directly with the process by which the stem is produced in the Y-shaped figures we have been considering.

In one important respect these budding processes resemble each other; they stand, namely, for a certain disorganization (how

produced may, for the time, not detain us) in the original physiological system. In another respect they differ, in that they lead, in the one case, to a hydranth, or part of a hydranth, in the other to a holdfast. This difference is essentially an expression of the different conditions controlling their development, of which the influence of adjacent parts is the chief. The intimacy of this cöordination is obviously a function of the physiological isolation

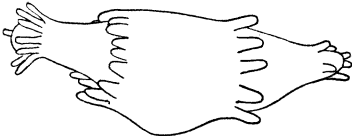


FIG. 13.

of the parts concerned. It is a conspicuous fact that Y figures are formed almost invariably from short heteromorphic segments; shrunk, starving, slow developing (Fig. 13, which shows

eth beginning of a bud) pieces give an especially large proportion of them. Frequently that portion of a segment of the column which lies against the floor of the aquarium puts forth tentacles more slowly than the upper surface. This retardation in develop-

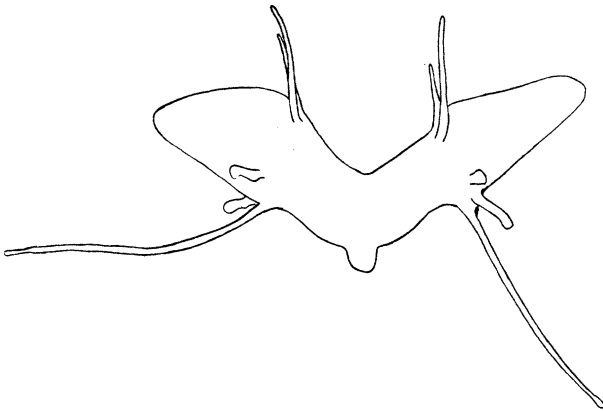


FIG. 14.

ment, due probably to diminished supply of oxygen next the substratum, is accompanied by a bending of the segment by means of a contraction of the affected side. It is on the opposite, convex, aspect of the column that the bud develops (Fig. 14, in which tentacles and gonads are only partly drawn), not, therefore, in direct contact with the substratum. And it is significant that, with the rarest exceptions that are referable to exceptional con-

ditions, such buds arising on heteromorphic pieces become holdfasts.

These facts indicate that while the origin of the bud depends upon a degree of disorganization in the original physiological system, its *fate* depends upon a secondary physiological coördination with the hydranths between which it develops. The bud acquires the distinctive character of a holdfast, namely, its adhesiveness, independent of any influence of the substratum. It has been pointed out already that a hydranth at one end of a piece exercises a profound influence upon the differentiation that may occur at the other end, depending on its own stage of development and its distance from that end. In the Y figures, then, there is a developing region between the two hydranths whose differentiation is controlled to some extent by them. An interesting case of the coördination of parts in a short piece developing as a Y figure, is represented in Fig. 15. A new axis at right angles to the original axis has been established. And the orientation of gonads and tentacles—especially the latter—is clearly a resultant of the redistribution of forces correlated with that change.

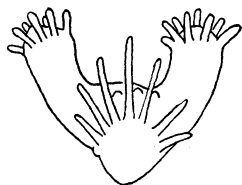


FIG. 15.

Fission may be considered as a special case of budding, depending upon the length of the heteromorphic piece involved. As the piece lengthens the tendency to bud vanishes, until the characteristic of adhesiveness alone remains. This indicates that the region between the two hydranths is still controlled by them, while the constriction and the frustules on either side of it (Fig. 10) mark the increasing effectiveness of their independence—or of the systems of which they form important parts.

It is only on heteromorphic pieces of moderate length, however, that fission of this type has been observed. Just as it was from relatively short heteromorphic pieces only that the reversals described in the previous section were obtained, the proximal elements of the longer pieces failing to produce holdfasts at the wound, so it has been only in the shorter heteromorphic pieces that the column between the hydranths has shown any signs of budding, constriction or frustule formation.

The longer pieces failed to differentiate in these directions, although attempts were made to encourage such developments, as follows:

1. Nine long heteromorphic segments were held against the aquarium bottom by weighted glass needles laid across their middle. One was cut in two in two days; neither portion had developed frustules twenty-four hours later. One was cut in two in three days; both portions had aboral processes, but no frustules developed in the following twenty-four hours. Four escaped from their needles on the third day, and showed no change at the end of another day. One was almost cut through by the needle, and three processes were formed at the wound, but no frustules or adhesiveness at the end of another day. One remained under the needle unchanged for four days, when the experiment terminated with my departure from the laboratory.

2. Discontinuity was produced by ligature on 16 long heteromorphic pieces two days-after regeneration had begun. In two days, 3 had broken into two parts. Two days later, 6 more had done so; the next day, 7 more. Seven days after the ligatures were applied, 2 had frustules at the ligatures. Both were contracted and opaque—signs of structural degradation; 3 possessed no frustules at the ligature; on the contrary, the proximal segment of one possessed a hydranth there. All the other ligatured pieces had separated into two portions, 18 in all, of which but 4 were attached aborally and possessed frustules.

The first of these experiments serves to emphasize the feebleness of contact as a formative influence, while the second adds to the evidence that differentiation in the region between heteromorphic hydranths depends in an important degree upon the distance between them, which other things equal, is an index of their control.

That the longer pieces do not show signs of fission, then, is to be attributed, I believe, to the freedom of the intermediate region in each case from the effective control of the physiological systems on either side, that may be conceived as extending over it from opposite directions. Where these systems are near enough together, a new compound system is created, of which a bud may form a part. When farther apart, their disharmony may appear in the phenomena of fission.

These statements are obviously very general. Since all short heteromorphic pieces do not either bud or divide by process of fission, there must be a factor still undefined that determines the lack of uniformity. There is no doubt that external agencies can facilitate either budding or fission. Small wounds in the side of the column may lead to a variety of results, including sporadic tentacles, and buds furnished with tentacles or frustules, or neither. In this connection two heteromorphic pieces, cut in the middle region, half way through the column, gave the following results. On the longer piece, a narrow bud developed in four days at the wound, with neither frustules nor tentacles. On the shorter piece, frustules developed around a blunter bud at the wound, before attachment took place. In this case, the wound was sufficient to break up the original system existing at that point and initiate a new development. The fact that frustules appeared shows the control of both hydranths on that development.

Budding occurs, however, when there is no sign of local injury from without. And it is difficult to account on this ground alone for the fact that the large majority of buds arise approximately midway between the hydranths. To my mind, far more significant is the fact that buds develop so often on pieces obviously in poor physiological condition *generally*. It is then that the physiological continuity of the piece through the transitional middle region might be expected to be especially affected by disruptive tendencies springing from the antagonism of proximal and distal systems—so obviously antagonistic in the fission shown in Fig. 10. In that case, the canals are completely obliterated at the constriction and the tissue is opaque and apparently impoverished. This constricted region is under tension, which probably accounts in part for its form. The tension is produced by the active migration of the two polyps away from each other, in the manner of the opposite halves of an anemone in process of fission by rupture.¹ The initial discontinuity is thus accentuated by the activities of the polyps themselves.

¹Torrey, *Univ. Calif. Publ. Zool.*, 1 (1904), p. 211.

IV.

Discontinuity can be established experimentally not only by the knife, which entails a wound, but, as already indicated, by ligature, by the use of which a wound can be avoided and conditions obtained that more nearly approximate those described in the last section.

This method has been used on *Tubularia* by Driesch, Morgan, Loeb, and Morgan and Stevens, and results obtained which are of interest in the present connection. By ligating segments of the stem, not only is the production of aboral (proximal) hydranths assured, but accelerated; and only exceptionally, after much longer periods, is there any development at the ligature itself. Loeb succeeded in showing that the acceleration of the development of the aboral hydranth is an indication of reversed polarity that exhibits a certain stability in regeneration. This is in accord with what I had already observed in *Corymorpha*, where reversals of polarity accomplished without the aid of the ligature are even more marked.

The experiments with ligatures have been repeated so many times on *Tubularia*, that it is hardly necessary for me to refer at present to similar experiments of my own farther than to say that the ligature accelerated the development of the aboral but not of the oral hydranth, and in no case was there any development at the ligature, on either side of it.

In Corymorpha, as in Tubularia, ligatures accelerate the velocity of development at the proximal ends of segments of the column. The fact does not stand out with such dramatic clearness, however, partly because there is greater individual variation in rate of regeneration, partly because the time intervening between the appearance of distal and proximal hydranths is much shorter. That such an acceleration occurs can be shown by an experiment like the following: Segments about 2 cm. long were cut from the distal half of 20 polyps, a ligature being passed tightly around each near its distal end. Segments of similar length were cut from the distal halves of 21 polyps of similar size; these were not ligatured. All were placed together in the same dish. In 28 hours, there were signs of proximal hydranths on 13 ligatured segments, and 14 on non-ligatured segments. The condition of

affairs at the end of 56 hours is shown in the following table, in which the serial numbers represent stages in the development arbitrarily selected for purposes of classification. Under each of these appears the number (1) of proximal hydranths in that stage of development on the ligatured segments, (2) of proximal hydranths on non-ligatured segments, and (3) of distal hydranths on non-ligatured segments.

TABLE I.

Dev. stages.....	1	2	3	4	5	6	7	Totals.
1. Lig. (pr.).....	0	5	3	5	5	1	1	20
2. Non-lig. (pr.).....	4	4	5	6	1	1	0	21
3. " (dist.).....	3	2	8	4	1	2	1	21

In spite of the individual variation represented by these figures, they show a tendency in the proximal ends to develop hydranths somewhat more rapidly on the ligatured segments, and almost as rapidly on the latter as the distal hydranths on non-ligatured segments.

V.

Although *Corymorpha* responds proximally like *Tubularia* when segments of the column are ligatured as above, there is an important difference in its response at the ligature, namely, in the rapidity with which hydranths are formed immediately below it. In *Tubularia*, a hydranth very rarely appears immediately below the ligature, and then only after the lapse of many days. In *Corymorpha*, on the contrary, hydranths form readily and frequently in this position.

That a hydranth should arise immediately below a ligature in *Corymorpha* might be anticipated from the occasional occurrence of such monsters as that shown in Fig. 16, which represents a regenerating segment of the column.

The proximal hydranth (below the angle) is not so far along as

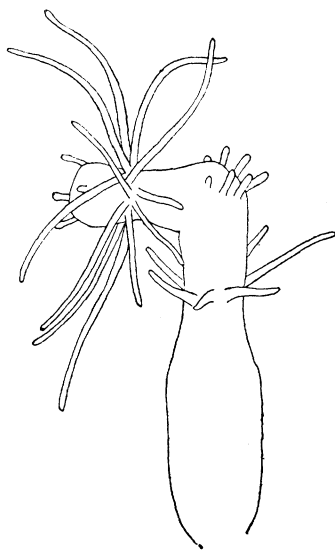


FIG. 16.

the distal hydranth, and has apparently developed later, below an interruption in the physiological continuity of the column comparable with what a ligature might produce. In fact, just such cases have been produced experimentally several times. A typical experiment may be recorded, showing incidentally the difficulties that made the number of positive cases so small.

The column of *Corymorpha* is very mobile, capable of considerable changes in length and bulk, and its tissues are very delicate and easily ruptured. So it has been difficult to make ligatures tight enough to interrupt the currents in the canals, as well as possible diffusions through the axial cells, without so weakening the column as to lead to complete rupture in two or three days. This has been accomplished, however, in a number of cases sufficient for the present purpose.

EXPERIMENT I.

April 29, 1910, 3.30 P. M. Sectioned 20 polyps of similar size, about midway of the column, and ligated each just below wound, leaving a small segment of tissue above the ligature.

May 1, 9.30 A. M. Four stumps removed, ligature having come away with terminal button of tissue.

May 2, 5 P. M. Thirteen more removed for similar reason. There are hydranths on these stumps that seem to be too far along, under the conditions, for $31\frac{1}{2}$ hours (*i. e.*, assuming the separation to have occurred immediately after the previous survey of them, which is not probable).

Of the remaining 3, 2 show nothing below the ligature, while the third appears as in the semi-diagrammatic Fig. 17, which bears a striking resemblance to Fig. 16.

May 3, 9.45 A. M. The two hydranths of Fig. 17 have fallen apart.

May 4, 10.00 A. M. Of the 2 stumps showing no development below the ligature of May 2, one (*a*) has now budded a set of tentacles just below the ligature; the other (*b*) as before.

May 6. The tentacles of (*a*) are larger.

May 9. Still no change in (*b*). Exp. abandoned.

In a second experiment, 6 columns were tied as indicated in the diagram (Fig. 18, *a*), after removal of hydranth.

EXPERIMENT 2.

April 7, 3.00 P. M. Hydranths removed and columns tied.

April 8, 1.00 P. M. (a) Distal ligature and tip fragment (1) broken away in 2 cases. (b) The three segments have separated in 1 case. (c) 3 cases in original condition.

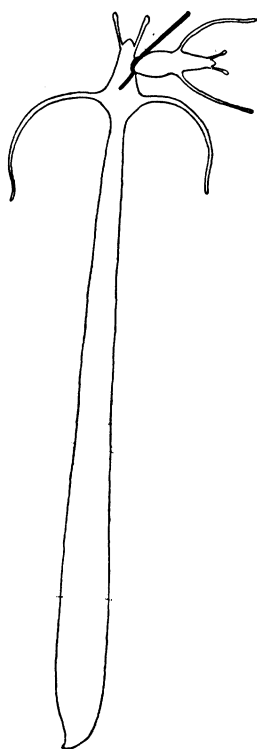


FIG. 17.

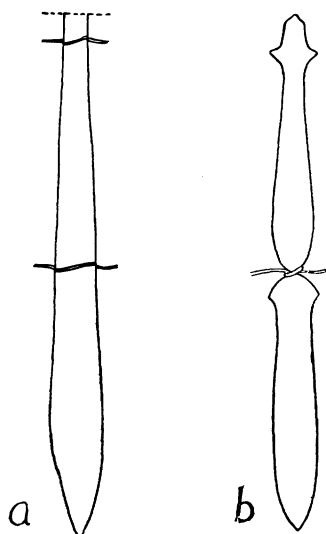


FIG. 18.

April 9, 2.00 P. M. (a) First case. Distal hydranth appearing on seg. 2, also on seg. 3 but not so far along. Second case. Distal hydranth appearing on seg. 2; not apparent on seg. 3, (b) —. (c) First case. The segments have separated while under observation. There are signs of a very slight rupture. and indications of tentacles on seg. 2 distally. Second case. The segments separated at 10.00 A. M. Seg. 2 shows signs of tentacles at both ends. In seg. 3, tentacles are being shadowed forth distally. Third case. The segments have separated,

seg. 2 showing faint signs of tentacles distally; seg. 3 in poor shape, removed.

April 10, 9.00 A. M. (a) First case. See Fig. 18, *b*. Note tentacles appearing just below ligature. Second case. Similar to first case; tentacles on seg. 3 not quite so far advanced.

April 11, 2.15 P. M. (a) Segments in both cases broken apart; exp. abandoned.

Of the six cases considered in this experiment, three show development of hydranths immediately below the ligature.

In a third experiment, the hydranth was removed from a polyp and the column ligatured near the cut and near the base. In three days, tentacles had budded just proximal to the distal ligature, as well as on the small distal segment. The next day, the latter was loosely joined to the segment proximal to it; both segments possessed hydranths with both sets of tentacles.

These results show that *hydranths form readily immediately below the ligature* in experiments like the foregoing.

VI.

The failure of *Tubularia* in such experiments to form a hydranth immediately below the ligature with the facility exhibited by *Corymorpha* is correlated with an important structural difference. The stem of *Tubularia* is encased in a stiff, chitinous layer of perisarc, that offers a certain barrier to the diffusion of gases between cœnosarc and the surrounding medium. The column of *Corymorpha*, furnished with a thin, rudimentary perisarc about its base, is naked for more than half its distal length; in this naked distal region, the ligatures were in all cases located.

When a ligature is passed tightly around a stem of *Tubularia*, the cœnosarc is not only ruptured, but the perisarc, itself intact in most cases, is drawn closely about each end of the cœnosarc thus produced. The result is that, while discontinuity has been established, the cœnosarc remains, as before, separated by the perisarc from the surrounding medium. When a ligature is passed tightly around a column of *Corymorpha*, discontinuity is established without in any way interfering in a comparable degree, if at all, with the diffusion of gases between cœnosarc and sea water. Now, when it is remembered that a discontinuity

brought about by a knife in *Tubularia* leads promptly to regeneration at the wound, the fact suggests that *Tubularia* develops with greater difficulty than *Cormyormpha* at the ligature because the coenosarc receives a smaller supply of oxygen in that region.

This view was tested by the following experiment, in which the factor of contact, which tends to inhibit development orally in *Corymorpha*, was eliminated.

Fifteen pieces, each about 2 cm. long, were cut from fifteen *Tubularia* stems of similar size and condition, just below the hydranth. The distal end of each was inserted in a capillary glass tube (closed at one end by a paraffine plug) into which it fitted easily, without terminal contact, *except with a small quantity of sea water*; the proximal end was free. As a control, 16 similar pieces were cut, both ends remaining free.

Forty-five hours later, the pieces in the tubes had developed nine hydranths on the outer (proximal) ends, nothing on the inner ends. In the control, though fifteen of the sixteen pieces possessed distal hydranths, no proximal hydranths were visible.

Twenty-five hours later still, all the pieces in the tubes possessed proximal hydranths; nothing had developed on the inner (distal) ends. In the control, only eight proximal hydranths were present.

Removed now from the tubes, all the pieces rapidly produced normal hydranths distally.

This experiment seems to establish (1) *that the failure of Tubularia stems to form hydranths, when ligatured, immediately below the ligature, is due to lack of oxygen*; (2) *that encasing the cut distal end of a stem in a glass cap leads to the same acceleration of development of the proximal hydranth as does the presence of a ligature*; and (3) *that accordingly, such acceleration is due to the inhibition of the development of the distal hydranth in the absence of an adequate supply of oxygen, rather than to an interruption of or other change in the course of the circulation in the canals*. The circulation is merely a transportation system, carrying substances favoring development that are removed from the stream by those tissues especially that have free access to oxygen, that is, by the tissues at the open ends of the perisarc tube. The possibility that oxygen might play such a role in this process of selection

was suggested by Loeb,¹ though in a somewhat different form in connection with a discussion of the function of the red pigment granules of the circulation.

The acceleration of proximal development in ligated pieces of *Corymorpha* is connected, not so much with any effect the ligature may have upon the supply of oxygen to the neighboring tissues, as with the inhibitory factors of contact and necrotic change that it introduces. The same factors may play a certain part in the inhibitory effect of the ligature in *Tubularia* also.

It will be remembered that if a piece of *Tubularia* or *Corymorpha* is ligated in the middle, development at the distal wound does not exhibit the acceleration characteristic of development at the proximal wound. This difference is to be explained, I believe, in the following way. Inhibition of development at the ligature on its proximal side hinders the utilization of a certain quantity of substances that would be used up proximally were the ligature not present. That the availability of this material for the distal end does not obviously accelerate the development distally is due, probably, to the initial acceleration of the distal over the proximal development in the absence of the ligature, that is, under conditions of active competition with the proximal end.

VII.

The considerations in the foregoing sections lead to the conclusion that the polarity of *Corymorpha*, of which the initial acceleration just mentioned is one expression, is a product of conditions under which the organism develops, changing as they change; that it is essentially but an inclusive designation for certain phenomena that depend upon both internal and external conditions, all of which can be experimentally controlled. The internal conditions appear in the effect of the continuity of tissue in an intact stem, and the presence of the original hydranth on a segment of stem, both inhibiting the development of a hydranth. The external conditions are represented by oxygen, contact, and necrotic changes such as are produced by ligatures. The first is necessary to all development while the others inhibit the development of the hydranth.

¹*Loc. cit.*

With the exception of the third, these are conditions that govern the development, whether embryonic or regenerative, and they are just the conditions by whose manipulation the original polarity of the column can be reversed. Since such reversal depends upon an acceleration of proximal relative to distal development, it would seem reasonable to suspect that a local acceleration in the development of the embryo might be the efficient cause of the initial polarity in the individual.

Such a local growth area appears in the embryo at the point which first leaves the egg case and thereupon defines the oral extremity.¹ This extremity may emerge at any point not adherent to the substratum; which qualification indicates that contact limits to a considerable extent the area in which the oral pole must appear. Since the egg case is a certain barrier to the diffusion of oxygen into the egg it is possible that variation in its thickness may be an important factor in determining the position of the oral pole in this area.

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August 9, 1910.

¹Torrey, *Univ. Calif. Publ. Zool.*, 3 (1907), p. 259.